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The North Kaibab Pandora Moth Outbreak, 1978–1984

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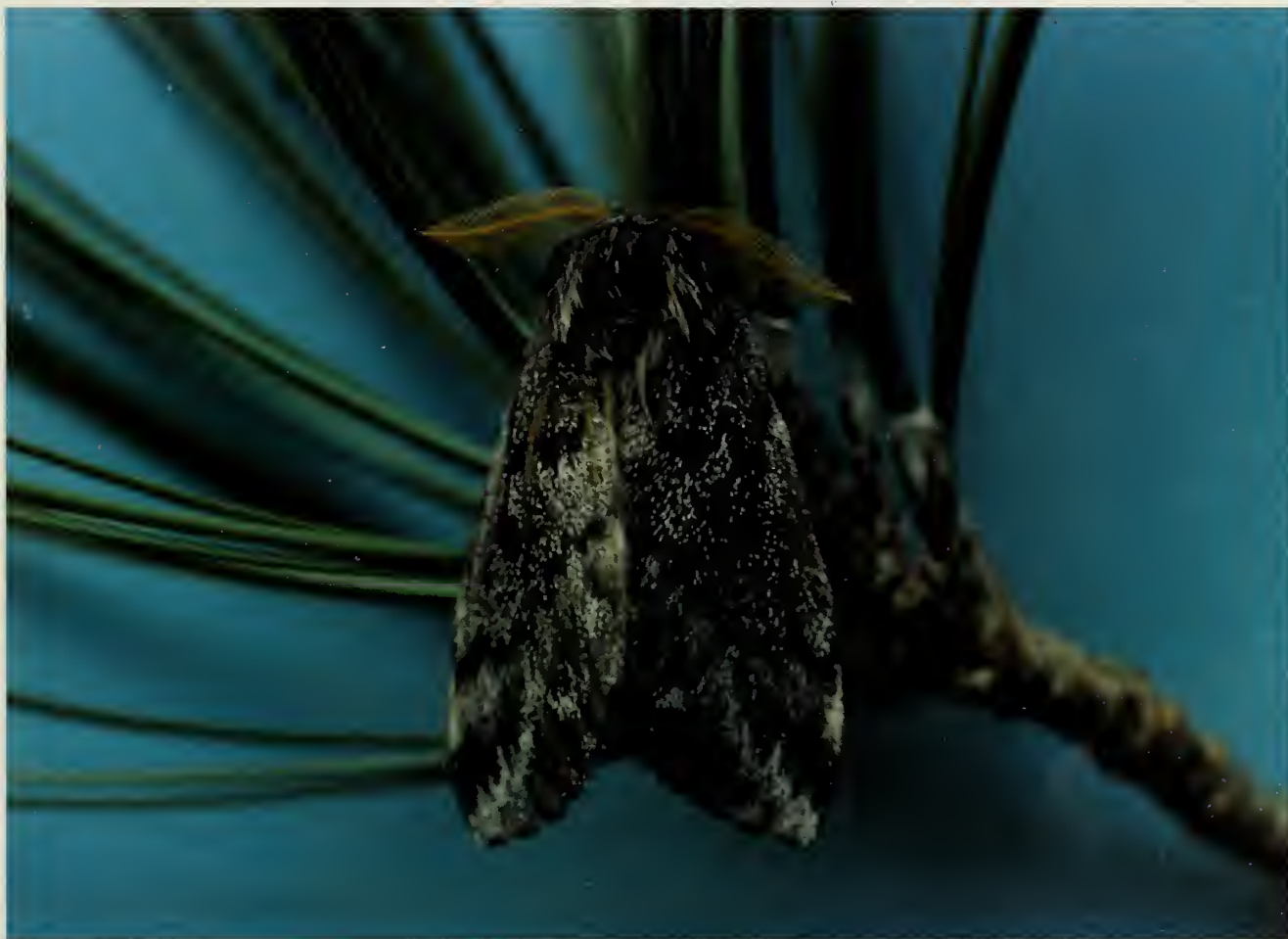
Small egg mass attached to ponderosa pine needle. Note head capsule appearing as dark spot on each egg.

Recently hatched first instar larvae and unhatched eggs.

The North Kaibab Pandora Moth Outbreak, 1978–1984

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Abstract

A pandora moth outbreak in Arizona was studied from 1979 to 1985 to determine the moth's life cycle, densities and distribution of life stages, larval and adult behavior, effects of the defoliation, sampling procedures, importance of biotic mortality factors, and the effectiveness of insecticides. This report summarizes the available published and unpublished information on the outbreak.

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Introduction

On August 1, 1978, a forester's son, accompanying his father during his field work, observed and collected several large moths in ponderosa pine (*Pinus ponderosa* Lawson) stands west of Jacob Lake, Ariz. (Sanders 1981). These specimens were later identified as pandora moths (PM), *Coloradia pandora* Blake. The moths, probably mostly spent males, were among the progenitors of larvae that caused the significant defoliation in 1979 and first alerted forest personnel to the outbreak. At the time, neither observer realized he was witnessing the beginning of the most extensive pandora moth outbreak recorded in Arizona and, perhaps, in the western U.S. This outbreak exhibited the classical textbook changes—an explosive population increase from an endemic level, followed by an equally rapid population decrease—all within four generations.

Although notable pandora moth outbreaks had occurred in California-Oregon (Patterson 1929) and Colorado (Wygant 1941), only limited biological information was gleaned from them. Key elements of the life history of this Kaibab population differed from previously reported information. Because the defoliation concerned forest managers, the North Kaibab outbreak was used to gather important new information and test hypotheses.

To simplify the presentation of information and reduce extensive descriptive phrases, the different generations and their respective defoliation areas are hereafter generally referred to as shown below and in figure 1.

Gen. I   August 1978–   Caused 1979 defoliation in
          August 1980   Defoliation Area I (DA I)
Gen. II   August 1980–   Caused 1981 defoliation in
          August 1982   Defoliation Area II (DA II)
Gen. III August 1982–   Caused 1983 defoliation in
          August 1984   Defoliation Area III (DA III)
Gen. IV August 1984–   Caused 1985 defoliation
          August 1986

The reader should not rigidly adhere to the above time periods, because, as will be discussed later, some exceptions do exist. However, for practical purposes, the generations are best described as stated above.

Extent of the Outbreak

Estimates of visibly defoliated acres provide one measure of the extent of the outbreak. Pine stands on 5,120 acres (2,072 ha) (fig. 1) were moderately (51–75%) or severely (76–100%) defoliated in 1979 (USDA 1980), while light (26–50%) defoliation was noted on several

Figure 1.—Defoliation areas during the outbreak.
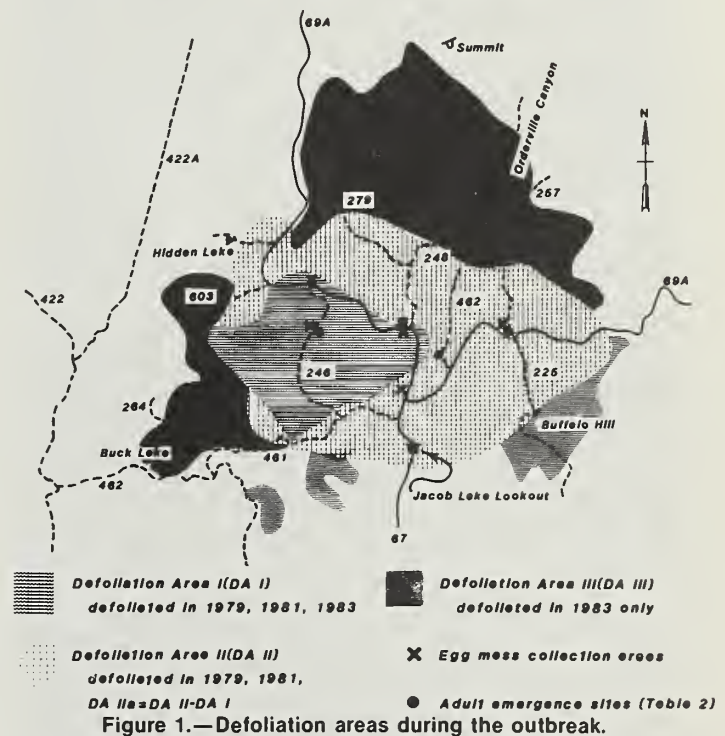
thousand additional acres. In 1981, approximately 18,700 acres (7,568 ha) were moderately or severely defoliated (USDA 1982); this area included the second defoliation of DA I. The 1983 area of defoliation covered 28,525 acres (11,544 ha), including most of DA II, but only 3,850 acres (1,558 ha) were severely defoliated. In 1985, no defoliation was observed during aerial detection surveys, although a few scattered individual trees in the peripheral area of DA III were observed from the ground.

During this outbreak, the combined areas of moderate and severe defoliation, as well as the estimated total acreage of defoliation, changed dramatically from one defoliation period to the next. For the different time periods, the ratios were as follows.

Defoliation periods	Defoliated area	
	Combined moderate and severe	Total estimated
1977:1979	1:>5,000	1:>8,000
1979:1981	1:3.7	1:2.2
1981:1983	1:.82	1:1.5
1983:1985	1:0	1:0

In both cases, although the area of observable defoliation increased with each generation, the rate of increase declined.

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The 1977:1979 ratio is the most interesting ratio, because it reflects the critical change from the endemic population to the outbreak level. However, the population may not have really increased to that level in one generation; rather, it may have increased to outbreak status in the unobserved August 1976–August 1978 generation preceding our Gen. I. This generation could have caused unnoticed defoliation over several hundred acres in 1977 and, subsequently, increased to the observable levels in Gen. I. Because the 1977 aerial survey of the North Kaibab Ranger District was conducted in early September, it may have failed to detect light to moderate defoliation in May because of July refoliation. Further, support of this "missed defoliation-generation" hypothesis came during the aerial detection surveys, flown August 1 and 2, 1985, when Bennett noted the difficulty of seeing pandora moth-caused defoliation at a new known outbreak location near Cape Royale, Grand Canyon National Park.

The extent of the outbreak is not fully characterized by the acres of defoliation. Adults were observed in Fredonia, Ariz., and Kanab, Utah—30 to 40 miles (48 to 64 km) northwest of Jacob Lake; Panguitch, Utah—110 miles (176 km) north of Jacob Lake; Marble Canyon and Lee's Ferry, Ariz.—40 miles (64 km) east of Jacob Lake; North Rim of Grand Canyon National Park—40 miles (64 km) south of Jacob Lake; Tusayan, Ariz.—55 miles (88 km) south of Jacob Lake; Cameron, Ariz.—114 miles (182 km) southeast of Jacob Lake; and Flagstaff, Ariz.—165 miles (264 km) mostly south of Jacob Lake (Tusayan, Cameron, and Flagstaff are south of the Grand Canyon). All but the North Rim location were disjunct from the original host type by at least 10 miles (16 km) of nonhost vegetation. Moths at all but the North Rim site were believed to have entirely dispersed to these localities on vehicles. While the only new infestation arose at the Grand Canyon site, the presence of moths at these other locations indicates the distances forest insects can spread when high population levels exist in a high-use recreation area.

Life Cycle

The life cycle lasted 2 years for essentially all of the pandora moth (PM) population. Moths began emerging in late July of even-numbered years. Peak numbers emerged around mid-August, and by the end of August over 99% of the moths had emerged. Less than 1% of the moths emerged in September or emerged the following year, which created a 3-year cycle. Moths were observed in October, but these were tattered males which probably had emerged in late September.

Egg masses (EMs) were laid shortly after adult emergence; thus, egg deposition lasted from late July through early September. Because the egg stage lasted at least 40 days and longer, unhatched masses found in October and November had been deposited in August or September.

Larval emergence began in late September and lasted into November, with most larvae emerging in October.

Most of the small number of unhatched egg masses noted in November were probably infertile or parasitized. First and second instars predominated in November of even-numbered years, with the second instar becoming the predominant stage during December and January. By mid-February, third instars could be found, particularly if above average temperatures occurred. As larvae more actively fed in April and May, they passed through the third and fourth instars until the fifth instar predominated in June. Fifth instars left the tree in late June and entered the ground to pupate. After entering the litter or soil, the larvae transformed to pupae through a prepupal stage during which they contracted in length and thickened in width.

Pupae predominated for the next 12 to 13 months, or roughly from July of the odd-numbered year until July to August of the following even-numbered year. Pupae were found after most moths emerged, but nearly all of these remaining pupae did not produce adults. A very small percentage emerged 1 year later, becoming the 3-year-cycle moths.

Oviposition Sites

Female moths oviposited on just about every conceivable object in the forest. Ponderosa pine was the primary site, with the egg masses predominately deposited on the foliage. The lower boles of trees 12 inches (30 cm) and greater in diameter (d.b.h.), particularly trees near light poles, received high EM densities (fig. 2). Pinyon [Pinus edulis (Engelm.)] and Rocky Mountain juniper (Juniperus scopulorum Sarg.) also were deposition sites in the natural forest. Egg masses stick well to needles and bark and were seldom dislodged during sampling, unless the needles or bark were broken off. Females did not confine their oviposition strictly to trees but also deposited eggs on cabins, rocks, and vehicles. Egg masses were particularly abundant on light poles, to which adults were attracted at night (fig. 3).

Immature Stages—Densities and Characteristics

Egg Numbers

Female moths were collected as they emerged and later dissected to determine the average number of eggs per female; the average number was 145, (range 108–188). Females with less than 100 eggs may have already deposited a cluster before examination.

Eggs were laid individually, and in groups of 2 to 38, but more than 20 and less than 3 were rare. Individual eggs adjacent to egg masses were probably either disconnected from the larger mass or resulted from disrupted deposition by a disturbed female.

The mean number of eggs per mass was 11 in 1980, but the modal number was 8 (Schmid et al. 1982b). In 1982, eggs per mass ranged from 3 to 30 (N = 105). The mean number per mass ranged from 11 to 15 in five different stands, while the modal number ranged from 9 to 12.

Location	Eggs per mass	Modal number per mass
"A" area	12.1 ± 4.6	12
Telephone plot	15.1 ± 5.0	11
"I" test		
Aug. 1982	11.1 ± 4.1	9–10
Oct. 1982	12.7 ± 5.3	12
Jacob Lake	12.0 ± 5.5	9
Burro Burn	12.8 ± 5.4	12

Eggs per mass were not significantly different between Gen. I and Gen. II (1980 and 1982). Eggs per mass were not studied in 1984, but the number per mass appeared the same as in previous generations.

Egg Mass Densities

Egg mass densities (EMDs) varied significantly among areas, depending on their defoliation status. In 1980, based on whole branch samples from trees ≥12 inches (≥30 cm) d.b.h., EMDs were not significantly different ($p = 0.06$) between severely and lightly defoliated stands (Schmid et al. 1982b). However, the mean EMDs for each crown level in the severely defoliated area were consistently greater than the respective densities in the lightly defoliated area, which suggests the differences might have been significant if additional samples had been taken. On trees 7 to 10 inches (18 to 25 cm) d.b.h., EMDs on whole branches were significantly greater in the severely defoliated area. In 1982, an egg mass evaluation, using one branch tip from each tree in forty-one, 5-tree clusters, indicated EMDs were greater in areas defoliated by the previous generation (Gen. II) than in areas severely defoliated by the two previous generations (Gen. I and Gen. II) or in essentially undefoliated areas (Schmid et al. 1983). Even though the population collapsed in 1983 during Gen. III, EMDs in 1984 were still significantly greatest in the area sustaining moderate to severe defoliation the previous year (1983) by Gen. III and significantly lower in areas previously defoliated two or three times or essentially undefoliated (table 1).

EMDs, throughout the outbreak, thus followed the pattern of defoliation—being significantly greater in areas moderately to severely defoliated by the previous generation and significantly lower in areas sustaining the same levels of defoliation by two or more previous generations or in undefoliated areas. The greater EMDs were present for only one generation in any specific area and, thereafter, declined to levels greater than the endemic level (i.e., ca. 0), but never as great as the previous high. These densities probably occurred because adult densities were greater there, and females oviposited more eggs in the area where they developed (Schmid et al. 1983). Females with a full complement of eggs may be too heavy to fly and, therefore, must deposit the majority of their eggs before dispersing.

EMDs were significantly different among trees in areas sustaining severe defoliation by two successive generations but were not different in the same size trees from areas sustaining other levels of defoliation (Schmid et al. 1983). The differences in the heavily defoliated area probably resulted from greater foliage production by some trees that were then more suitable as oviposition sites. During Gen. I and Gen. II, defoliation appeared uniform in most areas and did not differ significantly among trees. If stands were severely defoliated, then nearly all trees were severely defoliated. If stands sustained only light defoliation, then nearly all trees had light defoliation. However, during Gen. III, differential tree defoliation appeared as virus-caused larval mortality affected the PM population at different times.

EMDs varied significantly by crown level, depending on tree size and sampling unit. On both lightly and severely defoliated 50- to 80-foot (15- to 24-m) trees, EMDs were significantly greater in the lower crown than

Table 1.—Egg mass densities[1] ($\bar{x}$ ± SD) per branch, per nine shoots, and per 100 cm of branch length from undefoliated areas and areas defoliated one, two, or three successive times.

Sample unit	Years of defoliation[2]	Egg mass collection years		
		1980	1982	1984
Branch	0	7.5 ± 3.0 a	5.8 ± 5.1 a	0.4 ± 0.6 a
	1	10.2 ± 4.6 a	13.5 ± 10.6 b	1.5 ± 1.3 b
	2		7.0 ± 5.9 a	0.5 ± 0.8 a
	3			0.3 ± 0.6 a
Nine shoots	0		3.0 ± 3.0 a	0.4 ± 0.6 a
	1		7.5 ± 6.4 b	1.2 ± 1.1 b
	2		3.6 ± 3.5 a	0.4 ± 0.7 a
	3			0.2 ± 0.5 a
100 cm of branch	0		4.8 ± 4.3 a	0.4 ± 0.7 a
	1		11.4 ± 9.3 b	1.7 ± 1.4 b
	2		6.3 ± 5.6 a	0.6 ± 1.0 a
	3			0.4 ± 0.7 a

[1]Means within the same collection year and sampling unit, followed by the same letter, are not significantly different.
[2]Defoliation occurred in 1979, 1981, and 1983.

in the upper crown on a per branch and per foot of branch basis (Schmid et al. 1982a). Some of the difference on a per branch basis was attributable to branch size, the branches being considerably larger in the middle and lower crown. However, on the foot of branch basis, EMDs were greater in the lower crown.

On 25- to 50-foot (8- to 15-m) trees, EMDs were not significantly different among crown levels in either lightly or severely defoliated trees. EMDs per branch showed no trend in either defoliation class, but EMDs per foot decreased insignificantly from top to bottom in the lightly defoliated trees. These results differ from those of Buffam and Thompson (1964), who found significantly greater numbers in the upper crowns of 6- to 27-foot (2- to 8-m) trees. Because most of our trees were taller, the results are not wholly comparable. Further, their results indicated no significant differences between the upper and middle crowns. Thus, their middle and upper crowns may be comparable to our lower crowns so that crown level differences may not exist for 20- to 50-foot (6- to 15-m) trees.

EMDs on the foliage were not significantly different for the four cardinal directions within trees of the same size on specific locations (Schmid et al. 1983).

On the boles of large and small trees in a heavily defoliated area, EMDs were greatest within 1 foot (30 cm) aboveground. In lightly defoliated areas, EMDs were uniform throughout the first 20 feet (6 m) of large trees, but were greater in the first foot of smaller trees. The greatest EMDs were observed on the basal portion of light poles, because adults congregated on the poles during the evening hours (fig. 3).

Larval Instars

Head capsule width measurements indicated five instars were present during the larval stage. Widths for each instar ranged as follows.

Instar I	0.04–0.05 inches	(1.14–1.33 mm)
Instar II	0.06–0.08 inches	(1.56–1.98 mm)
Instar III	0.08–0.11 inches	(2.13–2.70 mm)
Instar IV	0.12–0.17 inches	(3.14–4.42 mm)
Instar V	0.18–0.23 inches	(4.65–5.90 mm)

Larval Densities

Based on branch tip samples, larval densities varied significantly between areas and among aspects within a tree but did not vary significantly among crown levels. Larval numbers were greater on the relatively level ridgetops than in adjacent ravines. These differences probably resulted from moth ovipositional behavior, which favored the environment of the homogeneous stands on the ridges.

Larval densities changed significantly among aspects as the larval period progressed. Just after egg hatch, first instar larvae were equally dense on all aspects. By late October, larval densities became significantly greater on the south sides and lower on the north sides. Larvae probably immigrated to the south to benefit from more favorable temperatures during winter. Larvae remained mostly on the south sides until the following April, when more larvae moved to northerly aspects. By mid-May, larval counts were greater on the north sides.

Larval densities in late October 1982 averaged 22 to 34 per 2-foot (0.6-m) branch tip in 10 stands severely defoliated in 1981, with counts of over 75 larvae per tip in some samples. In mid-May, larval counts averaged 3 to 4 per branch tip, with rare counts of 20 to 30 per branch tip. The larvae were much larger in size at this time, but overwintering mortality greatly reduced their numbers.

Pupal Dimensions

Female pupae averaged 1.3 inches (3.2 cm) long, with a range of 0.9 to 1.4 inches (2.2 to 3.6 cm) (n = 72). Male pupae averaged 1.3 inches (3.2 cm), with a range of 1.1 to 1.3 inches (2.7 to 3.4 cm) (n = 90).

The weight of female pupae averaged 0.09 ounces (2.7 grams), with a range of 0.04 to 0.13 ounces (1.2 grams to 3.7 grams). Male pupae averaged 0.07 ounces (2.1 grams), with a range of 0.04 to 0.13 ounces (1.0 to 3.6 grams).

Pupal Densities

Pupal densities varied with topography, canopy cover, litter depth, and proximity to trees. Densities were greatest on flat areas and decreased slightly when slope increased up to 10%; when slope was >10%, densities no longer decreased with increasing slope. Numbers of pupae were greater under an open canopy than a closed canopy (Miller and Wagner 1984). Densities also were greatest when litter depth was <1 inch (1 to 2 cm) but relatively equal throughout lesser and greater litter depths (Miller and Wagner 1984). Densities from plots ≥5 feet (1.5 m) from the bases of canopy trees were greater than from plots within 2 feet (0.2 m) of the tree bases (Schmid, unpublished); but, within 10 feet (3 m) of the tree bases, pupal densities were relatively equal. Densities also were equal on the four cardinal directions (Schmid et al. 1982b).

The pupal densities reflected the relative importance of site factors and larval behavior. Densities were greatest on the flat ridgetop areas with no or little slope, because this is where larval densities were greatest. As larvae descended from the crowns and departed tree bases, they apparently searched for pupation sites with 0.4 to 1.2 inches (1 to 3 cm) of litter. Beneath canopy trees, such areas usually were below the dripline of the crown where litter accumulation would be least and the canopy cover partially open. In pole and sawtimber sized stands, such areas were 10 feet (3 m) or more from the base of the tree, which accounts for the greater pupal numbers away from the tree bases than adjacent to them. However, litter depth may not have been the most important factor determining pupal densities. In 1980, Gen.

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I pupae were found in densities of 20 or more per square foot (215/m²) adjacent to the bases of sawtimber trees, where litter depth was 3 to 4 inches (7.6 to 10 cm). Frequently, larvae congregated in areas where litter depth was excessive or essentially absent, which suggests that larvae may leave some type of scent trail. Subsequently, pupating larvae might follow this trail and pupate in the same location. This could account for the high numbers of pupae found under tufts of grass when other adjacent tufts yielded no pupae.

During Gen. I and Gen. II, mean densities and the range of densities were similar. Gen. I pupal densities from three locations had mean densities of 3.0 per square foot (32/m²) and ranged from 0 to 32 per square foot (0 to 344/m²). Mean Gen. II densities were 1.2 near the bases of trees and 2 in areas more than 10 feet (3m) from trees; range equaled 0 to 30 per square foot (0 to 323/m²). Gen. III densities were not studied.

Moth—Behavior and Numbers

Emergence and Sex Ratio

In 1982, moths began emerging the last week of July (Schmid 1984). A few adults were observed around lights at Jacob Lake and some were caught in cages. The number of moths emerging daily continued at a low level until August 4, when the number increased substantially (fig. 4). Numbers generally increased thereafter, and maximum numbers of adults emerged during August 10–15. After mid-August, numbers decreased until August 30, when daily emergence averaged 1 to 2 adults per 400 square feet (37 m²) per day. Even at this low rate, over 100 moths per acre were emerging. Moths were observed on September 22, indicating a few moths emerged well after most of the population (99%) had emerged.

Moths at the 7,600-foot (2,316-m) elevation emerged about 10 days before the first adults appeared at 7,800 feet (2,377 m). The combination of higher elevation and

north aspect probably caused slower development at the higher elevation.

Moths emerged after late summer rains began on the North Kaibab. Rains apparently softened the dry, cementlike soil surface, allowing adults to emerge with less difficulty and, consequently, increased population survival.

Both sexes emerged during the first 10 days of the emergence period in 1982, but males outnumbered females by a 3–4:1 margin. As the emergence period progressed, the sex ratio shifted so it was essentially 1:1 during peak emergence and then 1:1.5 during the last 10 days of August.

Population Numbers

Based on emergence in 250 screen cages, each covering 1 or 2 square feet (0.09 or 0.18 m²), the number of moths emerging per square foot of ground surface ranged from 0 to 13 (table 2). Mean densities on ridgetops and midslopes were generally higher than in ravines, but a significant difference between ridgetop and ravine was not universally found. The low densities in ravine bottoms were expected, because previous observations indicated defoliation was less on trees there. The reason for this elevation variability is not known; but, because females are generally active only at night, and the ravine bottoms are noticeably cooler, females may be more active in the warmer thermoclines on the ridgetops and less active in the ravine bottoms. This explanation also may account for the broader pattern of infestation, wherein successive ridges had greater densities of larvae and greater defoliation than did broad, lower elevation areas between them (fig. 5).

The emergence pattern and trap catches of emerging moths reflect only a tiny proportion of the immense number emerging during an outbreak. If one moth emerged from every square foot of ground, then over 43,000 would emerge from each acre (109,220/ha). If this rate of emergence is assumed for the 19,000 acres (7,480 ha) moderately to severely defoliated by Gen. II larvae,

Table 2.—Number of emerging pandora moth adults per square foot of ground surface in 1982 (Schmid 1984).[1]

Site	FS Road 246 plot	U.S. Highway 89A plot	FS Road 482 plot	FS Road 257 plot
		$\bar{x}$ ± S.D.		
Ridgetop	0.4 + 0.8 a	0.8 + 1.2 a	2.4 + 3.2 a	1.7 + 2.4
Midslope	0.6 + 1.1 a	0.8 + 1.1 a	0.4 + 0.8 ab	
Ravine bottom	0.1 + 0.2 a	0.2 + 0.4 a	0.2 + 0.4 b	
		Range		
Ridgetop	0-3.0	0-4.0	0-12.5	0-13
Midslope	0-3.5	0-4.5	0- 2.5	
Ravine bottoms	0-0.5	0-1.5	0- 1.5	

[1]*Within columns, means followed by the same letter are not significantly different, α = 0.05.*

then over 800,000,000 moths would have flown in 1982. Considering the numbers observed around the lights at Jacob Lake, around the bases of trees and flying above the tree crowns at twilight, the multimillion figure seems valid.

Behavior

Moths crawled upward through the soil and litter from their pupal site, so the first evidence of their emergence was litter movement. After emerging, they crawled over the litter surface until they encountered any upward-oriented object, including tree boles, dead limbs, grass stems, *Solidago* sp., *Lupinus* sp., cones, and stumps. Most herbaceous plants failed to support an adult; when the stems broke or bent, sending the moth to the ground, it resumed crawling and either repeated this process with other herbaceous stems or eventually encountered a supportive object. Ninety-nine percent of the adults settled on ponderosa pine boles of all sizes.

Most moths settled on the tree boles a few inches to 6 feet (1.8 m) aboveground, with maximum ascension being influenced by tree size and, perhaps, the distance they crawled over the ground surface before reaching the tree. On seedlings and saplings, moths climbed to various heights and frequently climbed to the tip of the leader. On larger trees, moths settled various distances aboveground, ranging from a few inches (cm) to over 18 feet (5.5 m). Some moths that crawled for more than 30 feet (9 m) before encountering a tree settled within 3 feet (1 m) of the ground, and others that crawled lesser horizontal distances settled higher on the bole.

Moths seemed able to discern large trees when they were within 6 feet of them but seemed to encounter seedlings and saplings by chance. Adults frequently crawled past seedlings and saplings that could have provided suitable resting places and continued crawling until encountering another object. Large trees were not bypassed when the moth was within 6 feet (1.8 m) of them, but were when they were more distant.

Moths usually settled in a shaded spot on the tree where they could hang without their abdomen touching any surface and expand their wings. The wings are not fully formed when they emerge, but begin to expand once the moths settle into position; usually with a lateral rocking motion, during which the antennae are folded close to their ventrolateral surface just above the legs. The wings were expanded within 15 minutes. At first, the leading edge of the unexpanded wings were oriented laterally from the body. As they expanded, the leading edges came together over the dorsal surface of the abdomen and projected outward from the body. The wings remained in this position for another 30 to 45 minutes. Then the leading edges were brought to the lateral sides of the abdomen, and the trailing edges formed a triangular tent over the abdomen.

Moths usually remained in the same positions on the boles for the remaining daylight hours unless disturbed or unless their location became exposed to direct sunlight. In such cases, the disturbed moths frequently moved higher on the tree. On sunny days, adults emerging in the morning were usually found on the north and west sides of the trees. Moths emerging in the afternoon were found on the north and east sides of the trees. On cloudy days, more adults were seen on southern exposures.

During the first days of the emergence period, little flight and mating activity was observed. Few females mated during the wing expansion period, and no egg masses were observed on tree boles. As the emergence period progressed, more moths were present, and hundreds of males were observed flying during the daylight hours. Males frequently hovered 3 to 6 inches (7.6 to 15.2 cm) away from the boles and flew vertically or laterally around the circumference at this distance, apparently in search of females. Newly emerged females frequently mated as soon as they began crawling up the tree or while at rest during wing expansion. As a result, egg masses became abundant in the first 6 feet (1.8 m) of the bole. This probably accounts for the greater density of egg masses in the first 1 foot (0.3 m) of the bole as observed by Schmid et al. (1982b). Furthermore, the highly disproportionate sex ratio favoring males in the initial days of emergence decreases the possibility that females go unmated and apparently increases the chances of survival of the species.

Females generally were not observed flying during daylight hours. This observation, the tendency to avoid direct sunlight (fig. 6), and the tremendous nighttime activity around lights at Jacob Lake, indicates most adults, particularly females, are crepuscular and nocturnal. Males nearing death were the moths most active during daylight hours. Such males usually have lost most of their gray-black coloration and have frayed wings. The presence of discolored, tattered, fluttering but flightless males near the bases of trees indicated these males were spent, probably near death, and seeking to mate one last time. Contrary to Tuskes' (1984) hypothesis of a behavioral change associated with outbreaks, diurnally flying males of this outbreak probably were behaving the same as during endemic population levels, but their numbers made them more evident, while endemic populations are too low in number to be noticeable.

Moth-People Interaction

Neither the larvae nor the adults caused any skin irritations, such as those cited by Tuskes (1984); however, their presence was a considerable nuisance. Attraction of the moths to night lights annoyed tourists, recreationists, and workers at the Jacob Lake Inn and adjacent campgrounds. During the evening hours of August 1982, thousands of moths congregated around the lights illuminating the gas station, tennis courts, and cabins. Moths landed on people, vehicles, and buildings, in addition to the ponderosa pines. They were abundant enough to cause cancellation of tennis games and the early closing of the gas station. Because one outside night light was near the Inn's main entrance, moths frequently crawled into the Inn and onto people and furniture.

Figure 2.—High egg mass densities were found on the basal section of large trees.

Figure 3.—Artificially high egg mass densities were found on the basal sections of light poles.
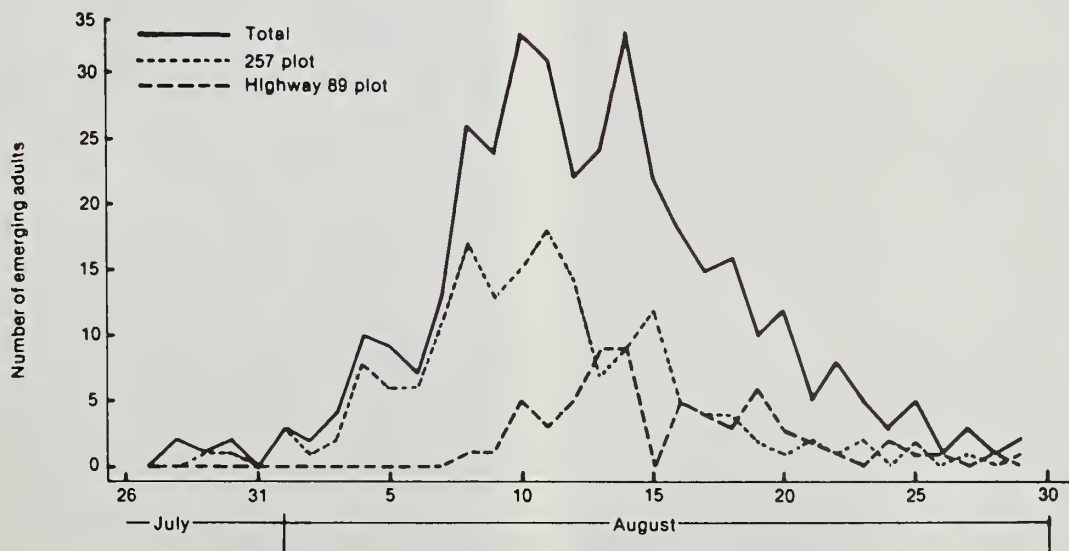
Figure 4.—Emergence period of pandora moths, 1982 (Schmid 1984).

Figure 5.—Color infrared photo of part of the defoliated area. Blue-green = defoliation; pink = nondefoliation.

Figure 7.—First instar larvae moving upward on bole. Note the single-file "follow the leader" behavior.

Figure 6.—Adults resting in shade on Jacob Lake Inn gas station. Note few are in the direct sunlight.

Figure 8.—Mature larvae moving toward the ground on the bole.

Figure 9.—Virus-infected larvae congregated around the leader of saplings.

Figure 10.—Mature larvae have consumed older needles but not new growth, which is just beginning.

Figure 11.—Severely defoliated trees were esthetically displeasing for only a few months because annual shoot growth began about the time defoliation ceased.

Figure 12. — Prescribed burning to kill PM pupae. Fires had to be burned at night (A) because conditions during the day were too extreme. Mortality was variable because the fire did not burn hotly throughout the area — note unburned areas in foreground (B).

Every morning following the massive nocturnal flight activity, especially during mid-August 1982, thousands of dead moths were swept up in the parking area immediately surrounding the main entrance light pole. Dead moths were so abundant that it was not possible to walk to the entrance without stepping on them—when the body was crushed, the noise was like popping popcorn. The accumulation of dead moths in a depression around one light pole combined with the abundant summer precipitation created a stench during August 1982.

Dispersal

Moth Dispersal

Moths disperse via their own ability and vehicular transportation. In natural dispersal, moths crawled from their pupal sites to nearby objects, generally trees, where they remained motionless while expanding their wings. Once the wings were fully developed, moths generally flew among the crowns the following evening, although females may have first crawled into the crowns before their initial flight. After wing expansion, moths were not seen on the ground again until they were so battered they could no longer fly.

The distance individual moths fly was not determined, but the area of defoliation provides a measure of distance. Between 1979 and 1981, the area of severe defoliation spread 4 miles (6.4 km) eastward. Moths were also seen over 10 miles (16 km) to the north, southwest, and south of the 1981 defoliated area, which indicates a distance for general population dispersal.

The presence of moths more than 25 miles (40 km) from the visibly defoliated area was probably caused by their transportation on passenger vehicles and logging trucks. The longer distances noted previously most likely resulted from vehicular transportation.

Larval Dispersal

Larvae dispersed four times during their life, including (1) within branch-tree, (2) north-south, (3) south-north, and (4) tree departure. First instars dispersed from the egg mass to the branch tips and usually clustered around a terminal bud. If the egg mass was on the bark of the bole, larvae moved upward on the bole (fig. 7) and then to the branches—a relatively great distance. If they were on the foliage, then the distance to the bud may have been relatively short.

First and second instars also dispersed from northerly aspects to southerly aspects in late fall. In October, densities of recently hatched larvae were relatively equal on all aspects, but by early November, larval densities became significantly greater on the southern aspects. This movement probably continued until over 95% of the larvae resided on southern aspects by mid-December.

As temperatures warmed in April and larvae fed more actively, they became more common on northerly aspects. In May, larval densities were greater on north-erly aspects unless virus-caused mortality greatly reduced the population. The greater northern densities are created by the movement from south to north—just opposite of the fall movement.

Final larval dispersal was the emigration of mature larvae from the foliage to the ground via the bole (fig. 8). In June 1983, 10 to 15 were observed descending on one aspect at any one time, and the general larval movement was downward. However, virus-infected larvae moved upward, apparently heading for the upper portions of the crown.

Biotic Mortality Factors

During the course of the outbreak, several mortality factors were noted but only superficially assessed. Insect parasites were important during the egg, larval, and pupal stages; a virus decimated the larval stages in Gen. III; and birds and mammals preyed on larvae, pupae, and adults.

Virus

The most important mortality factor was a virus, probably the same or one similar to the polyhedral virus cited by Wygant (1941). In 1980, the incidence of virus was low and so was mortality. Stelzer's evaluation in 1981 showed 3% of the larvae in DA I were virus-infected (Stelzer 1981). By June 1981 during the late instars, viral-infected larvae were evident throughout DA I where high density larval populations were present during Gen. I and Gen II. In 1983, the virus spread throughout the population and caused a dramatic population decrease. Initial virus prevalence rates for larvae hatching from egg masses collected in September 1982 averaged 5.2% for all areas but reached 11% in DA I and 10% for DA IIa (Bennett and Andrews 1983). Bennett and Andrews (1983) concluded that a viral epizootic was unlikely to develop throughout the entire infestation, although substantial mortality was to be expected in DA I and DA II. A subsequent collection of predominantly second instar larvae in March 1983 indicated an average virus prevalence rate of 36% at 21 days after rearing started, with 77% of the larvae affected (Stelzer 1983). Stelzer expected epizootic infection rates when the larvae reached maturity and correctly predicted population collapse in 1983.

How the virus spreads throughout the population and why it did not drastically reduce Gen. I and Gen. II populations was not determined. Stelzer (1986) hypothesized that virus residues originating from previous, undocumented PM outbreaks remain viable in the soil but not on the foliage. At the initiation of the current outbreak, Gen. I adults acquired small amounts of virus while emerging from the soil and litter. Females contaminated the external surface of the eggs during oviposition. Infected larvae contaminated the foliage during feeding and at death, but foliage also may have been contaminated via dust. Noninfected larvae contracted the virus by their contact with infected larvae or their ac-

tivity in the foliage frequented by the infected larvae. Because larvae usually disperse within the crown at least twice, the probability of contact between infected and noninfected larvae is great, and the incidence of virus-contaminated foliage increases. Eventually, the microenvironment of the PM is thoroughly contaminated such that essentially all of the population becomes infected and the population collapses.

Virus-infected larvae are usually sluggish, fail to respond quickly to disturbance, and usually just remain in the same spot, rather than crawling off when nudged (Wygant 1941). The bodies of dead larvae are flaccid and the integument ruptures easily revealing a liquid interior. Virus-infected fifth instars on saplings frequently move to the terminal portion of the leader and congregate around it (fig. 9). On the larger trees, such larvae move upward, rather than downward as healthy larvae do.

About 50% of the pupae collected in 1980 and 1982 failed to mature. The internal contents, a yellowish-green liquid, lacked any definitive structure. This condition may have been caused by virally infected larvae that formed the exuviae but died before the adults were formed.

Parasites

Egg parasite.—*Telenomus* sp. (Scelionidae) was the most important egg parasite, with parasitism averaging 6% for Gen. II, 4% for Gen. III, and 56% for Gen. IV. Although the latter percentage was based on only 32 egg masses while the other information was based on 350 and 630 egg masses, respectively, the population collapsed during Gen. III so that the number of egg masses available for parasitism in 1984 was relatively low (see table 2). Assuming the *Telenomus* population did not suffer the same degree of population reduction as the PM population, the *Telenomus* adults would be abundant enough to create a high incidence of parasitized egg masses in Gen. IV. Egg mass parasitism was not significant during the first three generations but was significant in Gen. IV or the generation after the population collapsed.

All eggs within each egg mass were not always parasitized—parasitized eggs are black and easily distinguished from nonparasitized eggs. During both Gen. II and Gen. III, 55% of the eggs in parasitized egg masses were parasitized. In Gen. IV, the percent parasitism was not precisely determined, but appeared to be more than 75%. Thus, the level of parasitism remained the same through Gen. II and Gen. III, and then increased significantly in Gen. IV.

Larval parasite.—An unidentified tachinid fly was reared rarely from the fourth and fifth instars, and was not a significant mortality factor.

Pupal parasite.—An ichneumon wasp [*Cratichneumon unifasciatorius* (Cresson)] emerged from reared pupae and caused less than 1% mortality. The ichneumoninae usually oviposit into pupae. Since they habitually search the ground for hosts, this species probably detects and parasitizes pupae, which are close to the surface and not covered by either thick litter or more than an inch of soil.

Predators

Pupae were consumed by the Kaibab squirrel and probably other small rodents, but the mortality was not quantified. Robins (*Turdus migratorius* Linnaeus) picked off moths resting on the shaded portion of the Jacob Lake Inn Service Station during August. The moths are active at night and usually rest in shaded areas during the day. In this case, they had been active around a vapor light near the building corner the previous evening and were resting on the light-colored brick, which contrasted sharply with their gray-black bodies (fig. 6). Each robin alighted momentarily on the building's surface to capture an adult and then flew off. Under forest conditions, the adults would be almost invisible on the tree trunks and, therefore, a less susceptible prey for robins. Other passerine birds were not observed capturing PM adults, nor were bats.

Defoliation

PM defoliation is confined to the older needles, rather than the new shoots and foliage. PM larvae do not destroy the terminal bud or the new growth (fig. 10), even though the fifth instar stage generally coincides with the development of the new growth. Thus, defoliated trees gain foliage during the year of defoliation and the effect on the tree is moderated.

Ponderosa pines, ranging from saplings to the largest dominants, were defoliated. Pinyons were severely defoliated during Gen. III, when the outbreak reached the ponderosa pine-pinyon juniper ecotone. Juniper, Engelmann spruce (*Picea engelmannii* Parry), and white fir (*Abies concolor* (Gord. and Glend.) Lindl.) were not defoliated, even though larvae were observed on them. Whether the larvae starved or emigrated to ponderosa pine was not determined.

Significant defoliation occurred in April, May, and June of the odd-numbered years—1979, 1981, 1983. A small amount of feeding took place in November of even-numbered years and perhaps between December and April. Defoliation became increasingly apparent in late April and May, because the larvae were more actively feeding. In addition, needle consumption increased as the larvae matured, so defoliation became more apparent.

During the outbreak, defoliation varied within the infested area and on individual trees. During Gen. I in 1979, defoliation exceeded 90% on 2,700 acres (1,093 ha) and 50% on 2,400 acres (971 ha). Within stands, defoliation was fairly uniform within the crowns of trees of all sizes. During Gen. II, defoliation again exceeded 90% on all sizes of trees throughout the approximately 19,000 infested acres (769 ha), but defoliation was noticeably less uniform throughout the area, being particularly absent or low on sapling to pole-sized trees in the ravine bottoms and heavy on the ridgetops. This characteristic, noted by Beal (1938) in the Colorado outbreak, is apparently common to pandora moth outbreaks. Defoliation during Gen. III declined as virus-caused mortality

decreased larval populations. Although the extent of the infested area was about double that of 1981, defoliation generally averaged 20% to 30% throughout defoliation area III (DA III) (see fig. 1). Defoliation approached or exceeded 50% on the southern aspect but was less than 10% on the north side, so the average defoliation was 20% to 30%. Around the periphery of DA III, particularly in areas outside DA II where previous generations were either low or nonexistent, defoliation averaged 75% and exceeded 90% on some trees. Defoliation on these trees was fairly uniform on all aspects of the crown.

Effects of Defoliation

The sudden development and spread of the outbreak and the superficially devastating appearance of severely defoliated pines, (fig. 11), as compared to normally green, healthy pines, resulted in a great deal of concern by private landowners, concessionaires, representatives of the local timber industry, and the general public. Of major concern was the perception that the reduction in visual quality due to defoliation would adversely impact tourism and recreational use in the area. Also of concern was the possible adverse effect of defoliation on the Kaibab squirrel (*Sciurus aberti kaibabensis* Merriam), a state-listed "unique species." These squirrels are almost totally dependent on ponderosa pine for every aspect of their survival, and the question arose as to whether they would disappear from areas of severe and moderate defoliation. Another important concern was whether the defoliation would seriously devalue the timber in a sale area coinciding with the northern portion of the defoliation area. Thus, a variety of impacts were possible, including tree growth loss, tree mortality, wildlife alterations, visual quality reductions, and nuisance significance.

Tree Growth Loss

The PM defoliation caused significant tree growth loss. Both growth loss and mortality were influenced by defoliation severity and frequency. The initial evaluation conducted after the 1979 and 1981 defoliations indicated a 25% reduction in basal area (BA) growth over 4 years in stands defoliated twice (DA I), and no significant reduction in stands defoliated once (DA IIa) (Bennett and Andrews 1983) (see fig. 1).

During the outbreak, radial growth for all diameters was about 10% less in DA I and 7% in the area treated with acephate (Bennett et al. 1987). Adjusted radial growth for all diameters increased significantly in the undefoliated area during the outbreak, while growth in DA I and the treated area remained unchanged. Thus, the differences in growth rates among areas were caused more by a lack of increase in the defoliated area than by an actual decrease. Similarly, adjusted basal area growth in the undefoliated area increased significantly during the outbreak, while in DA I it did not change and the treated area increased insignificantly. The difference

in growth rates (ca. 10%) between DA I and the undefoliated area was confounded by coincidental intermediate cuts in the defoliated area. The cutting released some of the trees, allowing them to grow faster and thus mitigate growth loss caused by defoliation. The confounding manifested itself differently in trees <14 inches (<36 cm) d.b.h. and trees ≥14 inches (≥36 cm) d.b.h. In trees <14 inches (<36 cm), both radial and basal area growth were not significantly different before and during the outbreak within DA I, the insecticide-treated area, and the undefoliated area. However, growth rates of some trees in DA I increased substantially, which even though insignificantly different, indicated more rapid growth was occurring. In trees ≥14 inches (≥36 cm), radial and basal area growth in the undefoliated area increased significantly, while both rates changed insignificantly in DA I. Thus, trees ≥14 inches (≥36 cm) are more adversely affected by the defoliation than trees <14 inches (<36 cm), and thinning does not appear to mitigate their growth reduction. Based on a 10% decrease in growth rate, the estimated loss in f.b.m. production would be at least 11 f.b.m. per acre (0.07 m²/ha) per year.

Tree Mortality

Tree mortality was insignificant after two defoliation periods (Bennett and Andrews 1983) and after the outbreak collapsed (Bennett et al. 1987). Mortality in one mistletoe-infected stand was greater than the average for the infested area (see Wagner and Mathiasen 1985, and section on Defoliation-Mistletoe Interaction), especially among trees with a mistletoe rating of 5 or 6. In other mistletoe-infected stands, mortality appeared normal.

The incidence of bark beetle-caused mortality did not increase during or after the PM outbreak. Some bark beetle-caused mortality was noted in DA I; however, the amount was low and not significantly different than in DA II and DA III. The lack of subsequent bark beetle activity may have resulted from the above-average precipitation during the growing seasons of 1981 and 1983 and the PM feeding habits. While Patterson (1929) characterized the defoliated trees as weakened and very susceptible to bark beetle attack, their weakened state during this outbreak may have been moderated by the above-average precipitation, which reduced summer moisture stress. In addition, because PM larvae did not feed on new shoots and developing foliage, the trees recuperated during the summer following defoliation, even though they lost the older foliage during the prior spring months.

Defoliation-Mistletoe Interaction

The presence of southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopdum* (Engelm.) Hawksworth and Wiens) further accentuated the effect of PM defoliation on ponderosa pine. Radial growth of severely defoliated, heavily infected trees was less than

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the radial growth of defoliated, noninfected trees (Bennett and Andrews 1983). Basal area growth was reduced 15% more in infected trees than in noninfected trees (40% versus 25%, respectively), although this difference was manifested only in areas severely defoliated two successive times (DA I) and not in areas severely defoliated once (Bennett and Andrews 1983). Similarly, mortality of severely defoliated, heavily infected trees was greater than for lightly or noninfected trees when the trees were severely defoliated two successive times (Wagner and Mathiasen 1985). Mistletoe-infected trees were less able to tolerate defoliation than noninfected trees (Bennett and Andrews 1983, Wagner and Mathiasen 1985), with the degree of tolerance inversely related to the level of infection (i.e., the mistletoe rating).

Wildlife

District wildlife biologists observed a temporary decline in activity of Kaibab squirrels in moderately to severely defoliated stands. However, normal activity resumed when the stands refoliated, and population levels were not seriously affected. In addition, some bird and mammal activity increased within the defoliated areas.

Visual Quality

Severe defoliation in 1979, 1981, and 1983 reduced the visual quality of stands along a 10-mile (16-km) travel corridor of Highway 89A, a main thoroughfare through the Kaibab National Forest leading to the North Rim of Grand Canyon National Park. Because trees partially refoliated, visual quality was improved slightly within weeks of defoliation. Reduced visual quality lasted 2 to 3 months every other year and by 1985 was no longer evident. The important aspect of reduced visual quality was the inquiries from thousands of area visitors who expressed concern about the high density of larvae and the fate of the defoliated trees.

Sampling and Survey

Sampling

Because no previous sampling methods existed to assess population levels, methods were developed during the outbreak. These methods may benefit managers during future outbreaks.

For assessing the extent of the infestation and its general expansion, a systematic distribution of permanent egg mass plots in and around an infestation should follow a pattern espoused by Bennett (1982). At least 10 plots should be established within the area defoliated by the first generation if that area is 2,000 acres (809 ha) or less. Additional plots should be added in proportion to the additional acres of infestation. Additional plots also should be established for several miles in all directions from the boundary of the initially defoliated area, depending on topography and host type, because the

population can spread several miles from one generation to the next. The number of additional plots to be established will depend on the desired accuracy of the infested area boundaries and the number of sample trees per plot. If the extent of the infestation is to be defined on a sectional basis (i.e., 640 acres), then one plot per section is needed. For the additional 13,600 acres (5,504 ha) infested in 1981 (difference between 1979 and 1981), approximately 21 plots would have been needed. Additional accuracy will require more plots in proportion to the desired accuracy, but fewer sample trees per plot may be necessary to make the additional accuracy cost-effective.

Within each plot, the number of sample trees will depend on the number of plots and the sampling objective. Because the variation in egg mass numbers per tree was not generally significantly different among trees of the same size within a small area [0.1 acre (0.04 ha)], 1 tree per plot is sufficient. However, some investigators are uncomfortable with 1-tree plots because of possible zero counts and the lack of measurement of between-tree variation. Before the significance of the different sources of variation were known, Bennett (1982) used 5 trees per plot, which gave good estimates but was excessive in view of the insignificant variation among trees. Multiple tree clusters were used, because they minimized chances of zero counts from a plot. However, the concept of cluster sampling was violated in many stands where the trees were not in close proximity because of stand conditions. The decision for single- or multiple-tree plots thus becomes determined by the sampling objective. If the objective is to precisely determine the presence or absence of the infestation, then single-tree plots are preferable. If the objective is to determine population trend, as well as the presence of the infestation, then 2- or 3-tree plots are preferable. The number of plots to be installed will decide whether 2- or 3-tree plots will be used.

Sample trees preferably should be 30- to 50-foot (9- to 15-m) tall dominants or codominants, so sample branches can be taken 25 to 35 feet (8 to 11 m) aboveground. Trees of this size usually will have straight, foliated branches without excessive dichotomy. Larger trees will have similar egg mass densities, but branches will come from the lower crown, which usually are dichotomous and are not readily suitable for the 9-shoot system. Samples could be drawn from less than 25 feet (8 m) on many trees, but PM egg masses are readily discerned from 10 feet (3 m) away; therefore, to eliminate bias in branch selection, branches should be removed from above 20 feet (6 m).

The basic sampling unit for egg masses was the 9-shoot system. Because egg mass numbers increased linearly with increasing numbers of shoots (Schmid et al. 1983), a 9-shoot sample usually was large enough to minimize zero counts and yet be handled in the basket of a pole pruner. Counts from whole branches or on a 39-inch (100-cm) branch basis will give similar results but are not as efficient.

Based on the rearing of egg masses and defoliation estimates, the following method for predicting defoliation from egg mass counts was developed.

1. Egg mass count averaging ≤1 per 9-shoot sample
   from trees in a 3-tree plot . . defoliation ≤25%
   Egg mass count averaging >1 per 9-shoot sample
   from trees in a 3-tree plot 2
2. Egg mass count averaging ≥3 per 9-shoot sample
   from trees in a 3-tree plot 3
   Egg mass count averaging >1 but <3 per 9-shoot
   sample from trees in a 3-tree plot . . . Sample two
   additional trees; if average count for 5 trees still
   falls between 1 and 3, proceed to couplet 3; if
   average count is ≤1, defoliation equals ≤25%.
3. Percent parasitism of egg masses ≤10%, virus
   prevalence rate ≤3% . . . . . . defoliation ≥90%
   Percent parasitism of egg masses ≥50%, virus
   prevalence rate ≥5% . . . . . . defoliation ≤35%

Because the above method is based on data not primarily designed for the production of the method, its precision is questionable. However, we know that an egg mass-defoliation prediction scheme for the PM is more complicated because of the influence of the virus. During Gen. I and Gen. II, when virus prevalence rates were less than 3%, egg mass counts of three or more per nine shoots signified 90% or greater defoliation—a relatively straightforward relationship. During Gen. III, egg mass counts were similar to those of the previous generations, but virus prevalence rates rose to 36% at 21 days (Stelzer 1983), and the population in such areas later collapsed. Defoliation averaged 20% to 30%, with most defoliation occurring before most of the larvae died. Thus, the incidence of virus needs to be entered in the method unless the user knows what generation is of concern. If PM population always collapsed in the third generation, then a prediction scheme could be relatively simple—high defoliation associated with high egg mass counts for two generations and low defoliation associated with high egg mass counts in the third generation. However, Patterson (1929) implies outbreaks may last four generations, which means that the prediction method would be in serious error if three generations are assumed for every outbreak. This proposed system is independent of the generations and, therefore, more suitable for all outbreaks, even when pest managers may not know what generation is involved.

To assess late instar larval populations during biological evaluations or insecticide projects, either single-tree plots or 3-tree cluster plots are satisfactory (Schmid et al. 1982a). For evaluation of insecticide projects in specific stands or areas ≤50 acres, the systematic distribution of 50 single-tree plots is preferable. This design is just as accurate as the cluster designs, gives better estimates of the population level throughout the specific area, and, therefore, better evaluation of the overall treatment effect. It tends to give more variation to the estimate because of the greater possibility for zero counts. However, most zero counts are created by topographical features, which can be recognized and minimized. The 3-tree cluster also is satisfactory, practically eliminates zero counts, and may be more preferable when large areas ≥100 acres (40 ha) are being evaluated. It does not give the equivalent representation as the single-tree plots but may be more cost-effective,

depending on how the plots are located in relation to roads.

Both tree size, sample height above ground, number of branches per tree, and branch form should be as in the egg mass sampling. A 16- to 24-inch (41- to 61-cm) branch should be the sampling unit instead of the 9-shoot sample. This length provides the maximum foliated length that fits into the basket of a pole pruner. Late instar larval numbers are fewer and more easily dislodged than first instar larval numbers, so maximum foliage must be collected.

Larval numbers vary significantly by aspect, so the sampling plan must take equal numbers of samples from each of the four cardinal directions. Because late instar larval numbers are greater on the north aspects, samples drawn mostly from southerly aspects will underestimate larval densities, while samples drawn mostly from northerly aspects will overestimate larval densities. If the sampling is being conducted to evaluate the effect of insecticide treatment, it is desirable to record the aspect for each tree during prespray sampling, so the same aspect can be sampled from that tree during postspray sampling.

Aerial Sketchmapping

To detect PM infestations and evaluate PM defoliation, aerial surveys must be conducted in late June or early July. The North Kaibab outbreak may not have been detected before 1979 because the 1977 aerial survey was conducted in September. By August, PM defoliation is partially camouflaged by the current growth of ponderosa pine, which is unaffected by the PM. Hence, the new shoot growth tends to hide the presence of an infestation or the defoliation from the inexperienced observer, particularly light to medium defoliation characteristic of a beginning outbreak. Bennett personally observed this condition, as exhibited by a subsequent PM infestation in Grand Canyon National Park in 1985, and concluded that had he not known of its presence, he might not have detected it.

In addition to aerial sketchmapping, color-IR photos at a scale of 1:15,000 effectively discerned and more accurately delineated undefoliated, partially defoliated, and heavily defoliated stands (Ciesla et al. 1984). This photography was particularly useful in mapping the extent of different defoliation levels over large acreages and ascertaining the effects of insecticide treatments (Ciesla et al. 1984).

Suppression Strategies

Concerns of local concessionaires, timber industry representatives, and the general public led to demands for an immediate course of action, namely PM suppression. However, very little research had been done in the past to suppress PM populations, and no chemicals were registered for use against these caterpillars. Therefore, several strategies, including prescribed burning and insecticides, were tested to reduce pandora moth populations in the vicinity of Jacob Lake.

Prescribed Burning

Prescribed burning seemed a natural tool for controlling PM populations, because larvae pupate in the litter and first few inches of soil. However, fuel and weather conditions and management policy compromise the effectiveness of this technique to the point that satisfactory mortality usually cannot be achieved.

Late June and early July burning (fig. 12) killed about 60% of the pupae on three different locations, but mortality within each area was variable (Schmid et al. 1981). On average, mortality was greater near tree bases where litter depth and, thus, fuel were greater.

Early summer burning of stands where litter depth is not uniform and deep but is interrupted and sparse will not yield satisfactory mortality. Because a substantial number of larvae pupate where litter is nonexistent or is less than 2 inches (5 cm) deep (Miller and Wagner 1984), the fire does not heat these areas enough to cause mortality. In addition, pupae are deeper in the soil under litter depths of less than 2 inches (5 cm) than they are when litter is 6 to 8 inches (15 to 20 cm) deep and so are not as directly exposed to the fire. Fire management policy also precludes early summer burning, because when fuels are highly flammable and capable of generating high heat, conflagrations also are possible and forest managers are reluctant to burn.

Late September burning caused insignificant mortality to pupae (Schmid unpublished) and was less effective than early summer burning. Mortality near tree bases was not greater than away from tree bases. The effectiveness of burning in September and October (fall) also is hindered by fuel conditions. Fall burning is preferred by forest managers, because fuel and weather conditions are more conducive to slow-burning, easily controlled fires. However, the greater soil moisture caused by fall precipitation and the cooler air temperatures inhibit the fire from killing the pupae via direct burning, lethal temperatures, or dehydration. The very conditions that make fall burning more favorable to forest managers makes them unfavorable from a PM control standpoint.

Insecticides

Before 1970, insecticides specifically effective against the PM were unknown. In 1971, Lyon reported on insecticides tested against PM larvae in the laboratory and determined pyrethrins were good candidates for field testing. From 1971 to 1980, no further testing was conducted, so no effective compound was registered for PM control when the North Kaibab outbreak erupted.

In the fall of 1980, field testing of four chemicals via an aerial application simulator showed acephate and permethrin to be significantly more effective than carbaryl or dimilin against first instars on saplings. Based on these tests, acephate was selected for use in the pilot test against third and fourth instars in May 1981. Acephate applied at the rate of 0.75 pounds per acre (0.86 kg/ha) yielded mixed results in five spray blocks.

Unadjusted mortality averaged 56% in three blocks and 21% in the other two blocks (Bennett and Ragenovich 1982). However, in the check areas, mortality was 20% during the same time period, so adjusted mortalities attributable to the treatment were 36% and 1%, respectively. The overall mortality for the 1981 project was well below the acceptable level. Substantial snowfall within 12 hours after application caused poor mortality in two blocks and probably influenced mortality in the other three blocks. These results led to the stipulation that future insecticidal treatment would be conducted only when suitable weather conditions exist the day of application and no precipitation is forecast for the following three or more days. In addition, treatment of small blocks, such as the 500- to 700-acre (202- to 283-ha) parcels treated in 1981, does not insure protection for more than one generation. In 1982, egg mass densities in the treated blocks averaged 2.7 per nine shoots (Bennett and Andrews 1983), which indicates adults may have immigrated into a treated area to create pretreatment population levels.

Because of the poor results and the potential need for another insecticide treatment in 1983, further testing was conducted in October 1982. Acephate (Orthene Forest Spray) reduced first and second instar larval populations about 50% within 12 days after spraying in October, while dimilin, malathion, and carbaryl were not different than the control (Ragenovich et al. 1986). After 213 days, both acephate and dimilin were equally effective, while malathion and carbaryl were less effective.

Because acephate was most effective in the 1982 tests, it was applied again over 650 acres (263 ha) surrounding the Jacob Lake Inn on May 20, 1983. The objective of this treatment was to prevent severe defoliation in areas of heavy visitor use. Following treatment, defoliation was generally less in the treated area than in the nontreated, infested areas (Bennett et al. 1984). While both the 1981 and 1983 insecticide programs reduced populations and provided foliage protection where visual quality was concerned, they had little or no effect on the overall course of the infestation.

Two options exist for insecticide treatment of PM populations—a fall treatment against first and second instar larvae and a spring treatment against mainly fourth instar larvae. The fall treatment usually benefits from more precipitation-free days that are more satisfactory for insecticide application, although by late October, the possibility of suitable weather substantially lessens. Other advantages of the fall treatment are that early instar larvae succumb to lower dosages of insecticide than are needed to kill late instar larvae (see Robertson 1983a, 1983b), and fall treatment should prevent at least 25% of the defoliation that usually occurs between fall and spring. One disadvantage of fall treatment is that a late September-early October treatment will encounter substantial numbers of unhatched egg masses, so short-lived insecticides may not affect subsequently emerging larvae, whereas a May or spring treatment benefits from the presence of actively feeding larvae and no unhatched viable egg masses.

Silviculture

Because stand structure and tree size do not seem to influence female oviposition behavior or larval survival, silvicultural activities have little potential for suppressing outbreaks. However, silvicultural treatments that maintain desirable stocking levels and reduce the incidence of dwarf mistletoe will reduce growth and mortality losses. Intermediate thinnings at the start of the outbreak apparently mitigated growth impact (Bennett et al. 1987).

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A pandora moth outbreak in Arizona was studied from 1979 to 1985 to determine the moth's life cycle, densities, and distribution of life stages, larval and adult behavior, effects of the defoliation, sampling procedures, importance of biotic mortality factors, and the effectiveness of insecticides. This report summarizes the available published and unpublished information on the outbreak.

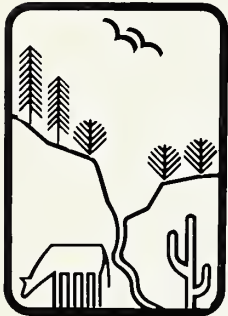Keywords: Pandora moth, *Coloradia pandora*, insect outbreaks, ponderosa pine

Top: V instar larva. Bottom: Prepupa and pupa in uncovered pupal site.

Rocky Mountains

Southwest

Great Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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Flagstaff, Arizona
Fort Collins, Colorado*
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Lincoln, Nebraska
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Tempe, Arizona

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